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Facultative hypothermia as a survival strategy during snowstorm induced food shortages in Antarctic storm-petrel chicks

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ABSTRACT

Wilson's storm-petrels (*Oceanites oceanicus*) are the smallest marine birds breeding in Antarctica, where events like snowstorms often prevent parents from providing food daily for their offspring. To minimize energy expenses, Wilson's storm-petrel chicks can reduce their metabolism and body temperature by entering hypothermia. Hypothermia is reported to impact development, hence we hypothesized that hypothermia will be majorly used after long fasting periods. Chick development in a breeding colony of Wilson's storm-petrels on the South Shetland Islands was monitored daily during three consecutive summers by recording chicks' body mass and temperature, as well as environmental parameters. Provisioning, and body conditions were highest in 2017, and chicks became hypothermic most frequently in 2016. Body temperature was influenced by age, mass, body condition, and minimal nocturnal temperatures. While most chicks were able to maintain stable body temperatures when not fed for one day, some chicks' body temperatures decreased by up to 21 °C. Age did not differ between those two groups, but chicks maintaining their active body temperatures had higher body conditions. Snowstorms were typically followed by several days of unreliable food provisioning and continuous days of fasting. Most chicks were hypothermic during this time, and were hence able to survive periods of food shortages, reverse their low body temperatures after the next feeding event, and regain body mass. We conclude that hypothermia is a strong survival strategy to endure times of fasting, which might be necessary for Antarctic storm-petrel chicks to reach adulthood. However, in future scenarios, which may include more frequent snowstorms due to climate change, malnourishment could lead to more frequent use of hypothermia, which could affect chicks' development.

1. Introduction

Many bird and small mammal species around the world can reduce body temperature to minimize energetic costs during resting (Geiser, 1998; Hwang et al., 2007; Schleucher and Withers, 2002). This facultative hypothermia and its energetic benefits range on a continuous scale from normotherm body temperatures to deep torpor, when animals appear lifeless and cold (McKechnie and Lovegrove, 2002). It can occur on a daily basis for some hours, as found in hummingbirds or several bat species (Geiser, 1998; Krüger et al., 1982). Hamsters, bats or storm-petrels can reduce their body temperatures during food shortages or cold temperatures for several days, when energy intake cannot cover the expenses for maintaining a constant body temperature (Boersma, 1986; Ruf et al., 1993; Wojciechowski et al., 2007). On the other hand it can be used to prepare migrating or hibernating animals for an energy demanding time to come (Geiser and Brigham, 2012). Next to these benefits also costs are associated with hypothermia. The lethargic state of torpid animals hinders immediate reactions when predators approach (Eichhorn et al., 2011; Hainsworth et al., 1977) and can result in predation, as shown for fork-tailed storm-petrel chicks predated by fungus beetles when torpid (Wheelwright and Boersma, 1979). Temperature controlled biological functions like enzyme-catalysed reactions can be slowed (Heldmaier et al., 2013; Hochachka and Somero, 2002). Furthermore, body temperatures affect the molecular structure of lipids and proteins, for example rendering biological membranes more viscous (Cossins and Prosser, 1978; Somero, 1995). Such biochemical changes influence many physiological functions and potential costs include metabolic imbalance (Jensen and Bech, 1992). During the reproductive cycle this not only affects adults' survival chances, but also their reproductive success. Depending on the phase of reproduction hypothermia can be beneficial or, on the contrary, harmful. In several bat species the sperm storage during winter seems to be benefitted by

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facultative hypothermia, as fertilization can be delayed for several months until the climate is favourable (Geiser and Brigham, 2012). During pregnancy, however, hypothermia can prolong gestation and hence is assumed to extending the development period of the offspring in bats (Audet and Fenton, 1988; Racey and Swift, 1981). Comparably embryos in storm-petrels are known to tolerate periodic chilling by several days of egg-neglect, but it will increase the total incubation time (Boersma and Wheelwright, 1979; Vleck and Kenagy, 1980). This delay of prenatal development can be risky, as it can put survival chances during the next winter or migration at risk (Ransome, 1989).

Hypothermic responses are not only found in adult animals, but also in juveniles. However, to use and profit from torpor or facultative hypothermia birds and mammals first have to establish the capability of active thermoregulation to maintain a stable body temperature in absence of food or a heat source (Geiser and Brigham, 2012). Altricial young show thermogenic responses in the early prenatal period, however they are not yet able to maintain a stable body temperature out of the thermo-neutral zone (Blumberg and Sokoloff, 1998). In precocial birds first endotherm reactions occur even before hatching and the effectors for thermoregulation are functional (Nichelmann et al., 1998; Nichelmann and Tzschentke, 2002). However, the efficiency is low (Nichelmann and Tzschentke, 2002). Hence, ability of active torpor or hypothermia use is unlikely. In between altricial and precocial animals range many seabirds that are considered semi-precocial: they hatch down-covered and show differing degrees of mobility, but depend on their parents' food delivery (Hamer et al., 2001). The efficiency of the endotherm system increases in species-specific times during the prenatal period (Nichelmann and Tzschentke, 2002). Some semi-precocial albatross and shearwater species show thermogenic responses within hours after hatching (Whittow, 2001). Others, like chicks of Wilson's storm-petrels are known to actively regulate their body temperature after five days (Gębczyński, 1995): in experiments chicks could maintain their body temperature at 5 °C ambient temperature for 30 min, afterwards one and three day old chicks' body temperatures and resting metabolic rates decreased, while five day old ones could maintain their resting metabolic rate and body temperatures. After thermoregulation is established hypothermia and torpor are used by juveniles in various situations. For example, juvenile Siberian hamsters used spontaneous torpor, potentially in preparation for winter, after weaning but before reaching maturation (Bae et al., 2003). In absence of food they were torpid at an even younger age. Likewise, nestling storm-petrels were reported to enter hypothermia in times of food shortages (Gębczyński, 1995). Once they are thermally independent, use of facultative hypothermia can be a powerful survival strategy. However, its negative impacts may weigh more for juveniles than for adults: depressed physiological functions during reduced body temperature may result in a reduction in growth and development (McAllan and Geiser, 2014; Racey, 1981). Thus, there is a trade-off between reducing energetic costs and investing in body functions such as growth and investment into immunology. Consequently, facultative hypothermia should be avoided as long as the nutritional state allows staying normothermic. In temperate areas hypothermia is often related to periods of cold or severe weather that make foraging impossible or decrease prey abundance (Doucette et al., 2012; Kunz, 1988). In regions like Antarctica prey abundance and therefore foraging success is probably usually not depressed by low temperatures (Quillfeldt, 2001), but weather extremes like strong winds or snowstorms, may lead to hypothermia due to fasting (Watson, 2013).

In the present study we examine hypothermia in a colony of the Antarctic seabird, the Wilson's storm-petrel (*Oceanites oceanicus*). Nestlings of Antarctic storm-petrels are semi-precocial and they are subjected to the combined stress of hunger (long intervals between feedings), cold, and long rest phases, making it potentially difficult to achieve a positive energy balance (Beck et al., 1972; Hamer et al., 2001). The regular use of hypothermia in petrels has been confirmed for one species breeding in temperate climate (Fork-tailed storm-petrels, Boersma, 1986) and one species in the Antarctic (Wilson's storm-petrels, Gębczyński, 1995). Wilson's storm-petrel chicks younger than five days entered hypothermia in times of food shortages (Gębczyński, 1995). Similarly, Fork-tailed storm-petrel chicks had reduced body temperatures while fasting (Boersma, 1986). Body temperature of smaller, younger chicks was found to be lower than body temperature of larger, older chicks, probably due to better surface-area volume ratios and feather insulation of the older ones. The more food the chicks gained the higher body temperatures could be observed. While food load or body temperature did not correlate directly with growth rates, higher variability in food loads that included large and small meals resulted in higher growth rates than more regular, but smaller food amounts (Boersma, 1986).

In this study we analyzed data along the temperature continuum between normothermic and hypothermic chicks. The term torpor was only used to describe animals that appeared completely lifeless. In particular, we tested the following hypotheses:

(1) Poor body conditions increase facultative hypothermia in Wilson's storm-petrel chicks. (2) Older chicks, with better insulation and better thermoregulatory capabilities, are less likely to enter hypothermia, and (3) facultative hypothermia will be more frequent after snowstorms.

2. Material and methods

2.1. Species and study site

Wilson's storm-petrels are marine birds that after fledging spend most of their lives offshore, but come to land for breeding (Quillfeldt, 2006). They are the smallest endotherms breeding in Antarctica, weighing on average 38 g and with a wing length of 15 cm (Beck et al., 1972; Quillfeldt, 2006). Their breeding colonies can be found in Antarctic and subantarctic ice-free areas, where the petrels most often nest in cavities below rocks (Quillfeldt, 2006; Roberts, 1941). They raise a single chick per year maximally and both parents participate in provisioning of the chick (Quillfeldt, 2006; Roberts, 1941). Depending on environmental conditions like snow cover, and parents' experiences chicks hatch between beginning of January and mid-March (Büßer et al., 2004; Quillfeldt, 2006; own observation). Like most petrels, Wilson's storm-petrels leave their young alone in the nest during the day at an early age, and majorly visit them during the night (Quillfeldt, 2006; Roberts, 1941). Adults often undertake foraging trips that last several days (Gladbach et al., 2009). During and after snowstorms nest sites might be blocked for several days and prevent adults to access their chicks (Quillfeldt, 2001). The study took place at a colony of Wilson's storm-petrels breeding in the scree slopes of the “Three brothers” hill about 1.5 km from Carlini Research Station on King George Island (Isla 25 de Mayo), South Shetland Islands (62° 14′ S, 58° 40′W). Monitored nests were all underneath big rocks and varied in depth from 20 cm to 60 cm. The monitoring period started each year a few days after the first chick hatched and lasted until the last ship left the station at the end of March. In 2015 the first chick hatched on Julian day 51 (median: 61), in 2016 on day 37 (median: 55), and in 2017 on day 18 (median: 30). Only in 2017 it was possible to observe nine of eleven chicks fledging. In previous years and for the other chicks we assumed successful fledging, if we found no dead chick in the nest the following season (2015: 6 of 6, 2016: 17 of 20, 2017: 22 of 24).

2.2. Monitoring and measuring of chicks

During the incubation period of three consecutive years we searched for active nests and measured eggs (length, width, mass). With these measurements we estimated their hatching dates according to Quillfeldt (2001) to avoid disturbing the parents during the incubation period by frequent nest checks. We looked for hatched chicks five days after this estimated date and afterwards monitored the first 20 chicks that

hatched daily until fledging/the end of the season while parents were foraging. When a chick died or was no more accessible during our observations we included a later hatched chick into the daily monitoring. Only chicks living past their 10th day were included into this data set. Analyses are based on data from 50 chicks monitored during three years (2015: 6, 2016: 20, 2017: 24). If adult birds were present at a nest, they were not disturbed and we checked the nest again the following day. We measured chicks' body mass to 0.1 g with a digital scale, and chicks' temperatures with a digital thermometer (Omega, HH506A, resolution 0.1 °C) and a connected thermocouple probe (Omega, Model HYP-2) in the cloaca, hereafter referred to as body temperature. We recorded breath rates by counting visible breathing for 10 s. Every three days we measured chicks' growth parameters: tarsus length to 0.1 mm using callipers and wing length to 1 mm using a stopped rule. The first measurements of each chick were used to determine its age following a logistic regression calculated from growth data from 1996 (accuracy for tarsus length 20 mm: 12.0 ± 0.3 days; Quillfeldt and Peter, 2000). With daily chick masses we calculated feeding rates and frequencies (i.e. food loads provided by parents, compare Gladbach et al., 2009), taking into account daily mass differences and the estimated metabolic loss during the day. If chicks appeared completely lifeless, we weighted them, and put them back into their nest immediately.

We analyzed body temperatures along the continuous gradient between 17 °C and 42 °C. The term torpor refers to chicks that appeared completely lifeless. We did not measure body temperatures in these birds.

2.3. Other

Wind speed [knt], and air temperature [°C] were collected at the local weather station located at the Argentinean Carlini station, and managed by their meteorologists eight times a day every 3 h, starting at midnight.

2.4. Data analyses

Statistical and graphical analyses were conducted in R (R Core Team, 2018; Version 3.4.4). Boxes of boxplots show data of the upper and lower quartile, their whiskers represent the 1.5 fold interquartile range from the box. The age independent parameter “body condition” describes the residual mass to the population mean mass of chicks of the same age, using data from ten breeding seasons (compare Quillfeldt, 2002a). Time of day is the time when we measured a chick's body temperature. Minimal nocturnal temperature was obtained from the weather station and was the minimal value between 1800 h the day before to 0600 h on that day. Accordingly, maximal wind speed was the maximal value during the same time.

We used a linear mixed effect model (R packages “lme4”; Bates et al., 2015, and “car”; Fox and Weisberg, 2011) to describe the influences of environmental, age, time of day, and provisioning parameters on chicks' body temperatures. The data were nested in chick identity and year as random effects to control for daily measurements of the same chicks during the study period and a possible family effect of chicks from the same nest in different years. To improve model fit body temperature data were ranked. Age, body condition, time of day, minimal temperature during the night, maximal wind speed during the night (all continuous), year (factorial) and fed (factorial, indicating if chick was fed in the previous night) were included as fixed effects, as well as an interaction between body condition and fed. We included variables and the interaction was based on biological reasons. No collinearity between fixed effects was found.

We tested the relation between chicks' body temperatures and the numbers of days without food with a Spearman's rank correlation for all data together as well as for medians per chick. With Kruskal-Wallis Chi-squared tests we analyzed differences of median feeding rate per chick, and median body condition per chick among years. For between year analyses we used Wilcoxon's rank sum test with continuity correction.

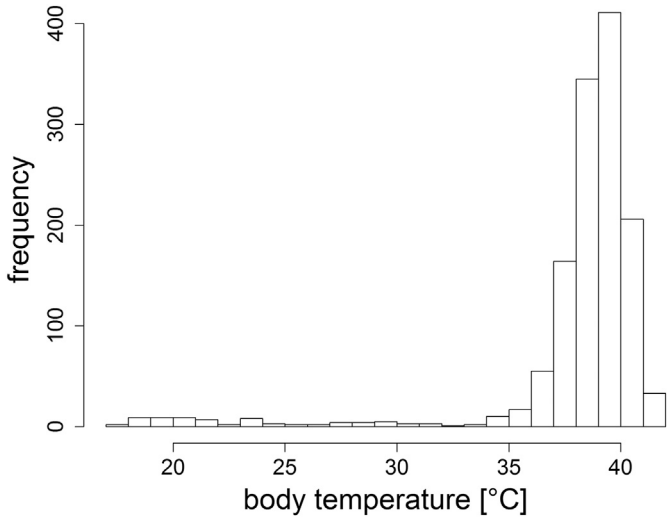

Fig. 1. Distribution of body temperatures (°C) for Wilson's storm petrel nestlings. > 90% of body temperatures from 50 monitored chicks ranged between 36 and 42 °C with a median of 39 °C.

3. Results

3.1. Body temperature variability and hypothermia

Over the three observed years body temperatures of monitored 50 chicks ranged between 17.7 °C and 42.0 °C (Fig. 1). The median of all measurements was 39.0 °C, 75% of chicks‘measured cloaca temperatures were 38 °C or higher, with < 10% of chicks being observed with body temperatures below 36.0 °C. One chick appeared cold and lifeless for 11 days. Five chicks maintained their body temperatures during three days of fasting (Table 1). Five chicks increased their body temperature by at least 4 °C without being fed (Table 2). The time of measurement did not significantly affect body temperatures, and older chicks had higher body temperatures than the young ones (Fig. 2; Table 3).

3.2. Influence of feeding and body condition

On average chicks were fed 5 g each night (Table 4). The amount of food that was provided to the chicks by their parents did not differ significantly among years (Kruskal-Wallis-Test: $X^2 = 5.2$, d.f. = 2, $p = .073$; Fig. 4), but chicks in 2017 received significantly more food than chicks in 2016 (Wilcoxon's rank sum test: W = 145, $p = .025$; Table 4). Body condition was highest in 2017 and lowest in 2016 (Kruskal-Wallis-Test: $X^2 = 23.0$, d.f. = 2, $p < .001$, N_{chicks} 2015: 6,

Table 1
Occurrences of fasting chicks for three days without drop of body temperatures. Table shows observed years, IDs, ages, the mass of the chicks before fasting, their mass loss during three days of fasting, the averaged mass loss per day for the three fasting days (± SD) as well as the average body temperature during those three days of fasting (± SD). Each line represents data from one chick.

Year	ID	Age [days]	Mass [g]	Mass loss [g]	Mass loss per day [g]	Mean body temperature [°C]
2015	1	25	53.15	15.91	5.30 ± 5.42	39.2 ± 0.2
2016	4	29	52.15	10.99	3.66 ± 3.87	40.0 ± 0.5
2017	5	32	46.88	12.95	4.32 ± 0.61	36.6 ± 0.9
2017	6	32	53.81	13.15	4.38 ± 2.68	40.0 ± 0.3
2017	7	32	56.62	16.84	5.61 ± 3.21	39.3 ± 0.2

Table 2
Occurrences of reheating after temperatures below the 90% range of body temperatures of 36 °C without feeding events. Table shows observed years, IDs, ages, the mass of the chicks before fasting, their mass loss during fasting, body temperatures before and after fasting, temperature differences and the time span during which this reheating was observed. Each line represents data from one chick.

Year	ID	Age [days]	Mass [g]	Mass loss [g]	Body temperature before fasting [°C]	Time difference [h]	Body temperature after fasting [°C]	Temperature difference [°C]
2015	2	8	25.88	−3.36	31.4	11	38.8	7.4
2015	2	10	31.20	−3.44	35.6	10	40.3	4.7
2015	3	18	54.01	−8.08	35.1	24	38.6	3.5
2016	4	12	32.19	−6.75	34.3	24	38.1	3.8
2017	8	7	25.97	−3.9	34.1	14	38.8	4.7
2017	8	51	69.82	−5.26	29.0	24	40.8	11.8
2017	9	28	62.13	−4.58	35.9	24	39.8	3.9

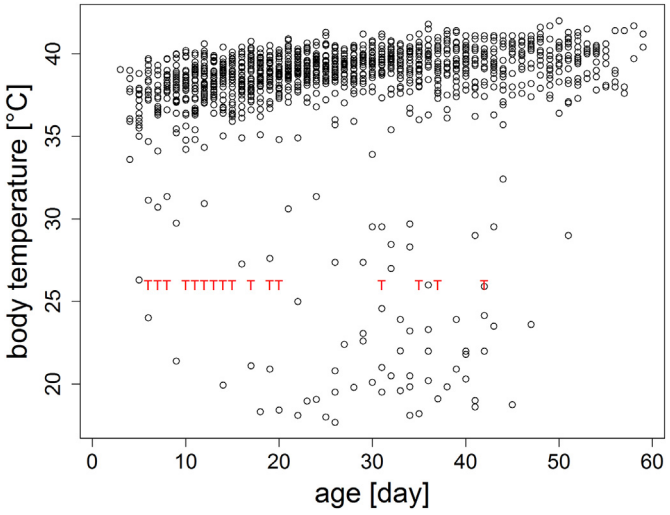

Fig. 2. Change of body temperatures of Wilson's storm petrel nestlings with age. Body temperature increases significantly with age (Table 3). Red "T"s represent torpor occurrences without temperature measurements (defined by visual judgment). Data come from 50 monitored chicks.

Table 3
Statistical values for linear mixed effects model of body temperature (dependent variable) in relation to body condition, age (days), the factor variable fed, indicating if chicks were fed or not during the previous night, time of measurement, minimal nocturnal ambient temperature (°C), maximal nocturnal wind speed (knt), the factorial variable year, and the interaction between fed and body condition. The model was nested for individual chicks (50) and years.

	F-value	d.f.	d.f. resid.	*p*-value	relation
Intercept	14.86	1	124.05	< 0.001***	positive
Body condition	63.45	1	1083.26	< 0.001***	positive
Age	117.94	1	1037.77	< 0.001***	positive
fed/unfed	3.89	1	1069.09	0.049*	positive
Time of measurement	1.14	1	1021.85	0.287	
Min. nocturnal temperature	4.71	1	1072.91	0.030*	negative
Max. nocturnal wind speed	0.06	1	1058.18	0.809	
Year	1.66	2	32.74	0.206	
Body condition: fed	51.03	1	1059.66	< 0.001***	

2016: 20, 2017: 24). Chicks with positive body conditions showed significantly higher body temperatures (Table 3). Chicks that received food in the night before had significantly higher body temperatures than unfed chicks (Table 3). After not being fed for at least one day body temperatures decreased with decreasing body conditions (Fig. 5, Table 3). Body condition did not affect body temperature for fed chicks (Fig. 5, Table 3). The highest temperature decrease was 21 °C and in 10% of observations chicks had temperatures below 36 °C (lower range of boxplot whiskers; Fig. 3), while in 57% of the observations from 47 out of 50 chicks they had a maximal temperature decrease of 1 °C

Table 4
Parameters for chick-provisioning (mean ± SD) for 2015–2017 for the monitored 50 chicks. Meal size shows the amount of food provided by one parent per night (g), feeding frequency shows the mean number of meals provided by both parents per night (meals/night), feeding rate describes the mean total amount of food one chick received per night including single meals, double meals and nights without feeding (g/night), and frequency of double feeding shows how often a chick received two meals when fed during the night.

	2015	2016	2017	Total
Meal size	4.46 ± 1.38	4.56 ± 0.84	5.52 ± 0.82	5.01 ± 1.02
Feeding frequency	0.78 ± 0.17	0.62 ± 0.13	0.78 + 0.11	0.71 + 0.15
Feeding rate	5.92 ± 1.79	5.35 ± 1.10	6.67 ± 1.06	6.05 ± 1.31
Frequency of double feedings	0.14 ± 0.07	0.18 ± 0.14	0.19 ± 0.09	0.18 ± 0.11
Maximal feeding rate	17.10 ± 4.77	16.50 ± 3.23	20.32 ± 2.84	18.41 ± 3.69

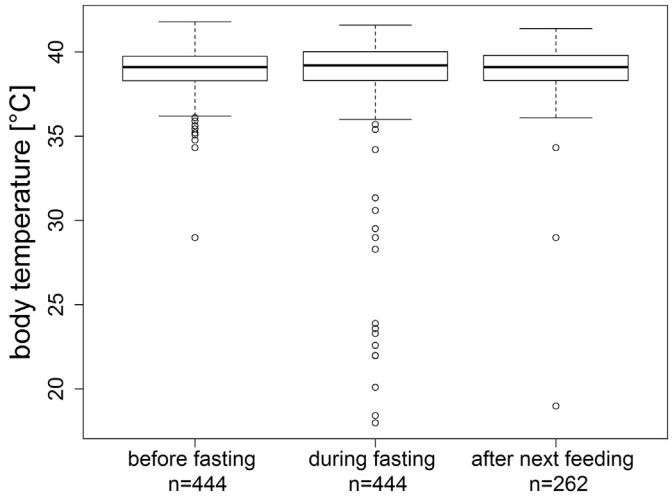

Fig. 3. Change of body temperatures of Wilson's storm petrel nestlings between fed and unfed chicks. Most chicks maintained stable, normothermic body temperatures during one day of fasting. However, some chicks decreased their body temperatures already after one day of fasting (middle column, 49 chicks) compared to the body temperatures when fed last (49 chicks). After receiving their next feeding most of chicks raised their body temperatures again (third column, 46 chicks).

(Fig. 3). After up to six days without feeding chicks' body temperatures increased after the following feeding event up to 19.8 °C (Fig. 3). In a total of 92% of observations we still measured temperatures above 36 °C before that next feeding (data within boxplot range; Fig. 3). If chicks were not fed for several continuous days their body temperatures declined significantly with increasing numbers of days without food

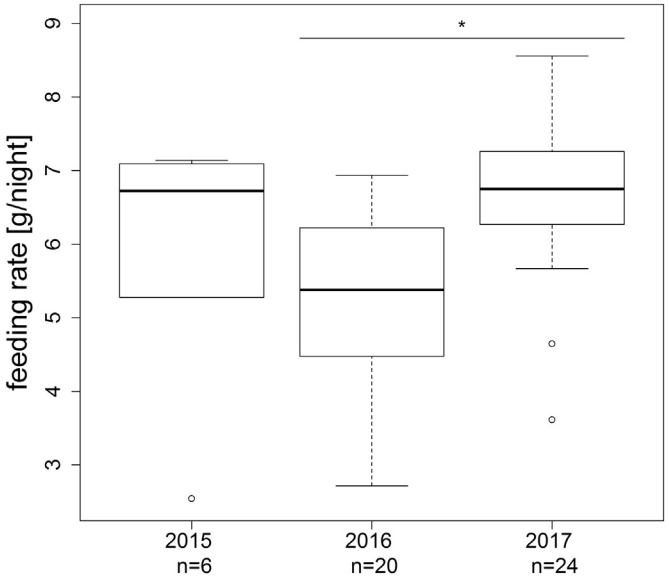

Fig. 4. Differences of provisioning in Wilson's storm petrels among years. Feeding rates (g/night) were significantly higher in 2017 (24 chicks) than in 2016 (20 chicks), but were not different from 2015 (6 chicks; compare Table 4). Significance is indicated by asterisk.

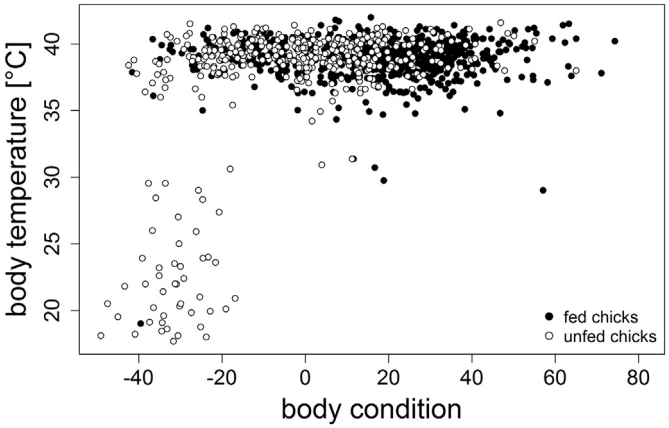

Fig. 5. Relationship between body temperatures and body conditions in Wilson's storm petrel chicks vary between fed and fasted chicks. Unfed chicks decreased their body temperature with decreasing body condition, while fed chicks maintained a stable body temperature (N_{chicks} = 50).

(for all data: Fig. 6; Spearman's rank correlation, rho = −0.067, S = 239,911,810, p = .026; for medians for each chick: Fig. 7: Spearman's rank correlation, rho = −0.190, S = 957,580, p = .013).

3.3. Influence of environmental conditions

Minimal nocturnal temperatures ranged between −6.4 °C and 4.5 °C, with a median temperature of 1.0 °C. Maximal nocturnal wind speeds had a median of 13 knt and measured between 0 and 65 knt. Chicks' body temperatures were significantly negatively affected by minimal nocturnal temperatures, but not affected by maximal wind speed during the former night (Table 3). Additionally, the later we measure a chick's temperature during the day, the warmer it was.

After two snowstorms within three days during the breeding season 2017 at the end of February we measured chicks again daily as soon as the nests had been excavated and accessible. During the following 10 days chicks experienced both, days of fasting and days of provisioning (Fig. 8). During these days after the snowstorms, 14 of 20 chicks decreased their body temperature by 10 °C (compared to body

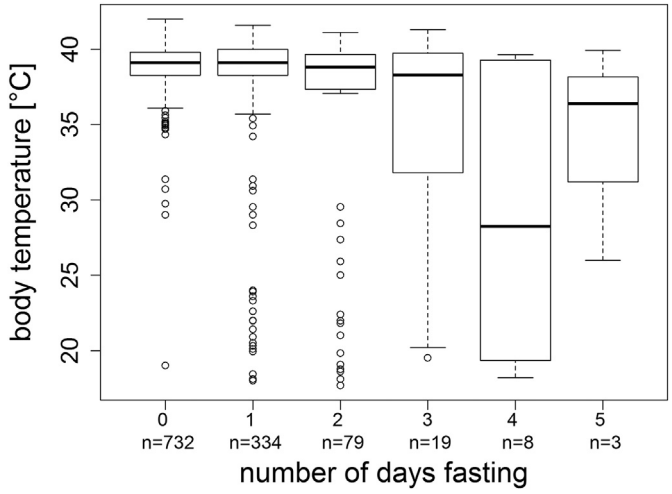

Fig. 6. Decline of body temperatures of Wilson's storm petrel nestlings during several days of fasting. Body temperatures significantly decreased when duration of fasting increased. N_{chicks} for 1st column: 50, N_{chicks} for 2nd column: 50, N_{chicks} for 3rd column: 40, N_{chicks} for 4th column: 18, N_{chicks} for 5th column: 8, N_{chicks} for 6th column: 3.

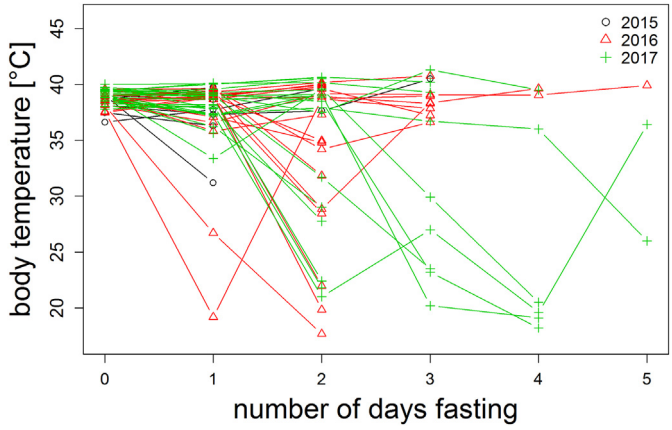

Fig. 7. Decline of body temperatures per chick during several days of fasting. Mean body temperatures of each chick were calculated for six groups: when fed during the night before (50 chicks), and after fasting for one day (50 chicks) until fasting continuously for five days (3 chicks). Different years are presented by different colours: black: 2015, red: 2016, and green: 2017. N_{chicks} for 3rd column: 40, N_{chicks} for 4th column: 18, N_{chicks} for 5th column: 8.

temperatures before the snowstorms) or more for at least one day, four chicks had body temperatures between 19 °C and 24 °C for three or more days. One chick died after several days without provisioning. All other chicks increased their body masses continuously again on average six days after the second snowstorm.

4. Discussion

The aim of the present study was to describe the variability of body temperatures in Wilson's storm-petrel chicks, in relation to provisioning, age, and environmental parameters such as air temperature, wind speed or snowstorms. We wanted to investigate when and why chicks were hypothermic and what characteristics this behaviour would show.

4.1. Body temperature variability and hypothermia

We found that Wilson's storm-petrel chicks growing up in Antarctica have highly variable body temperatures, ranging between 17 and 42 °C,

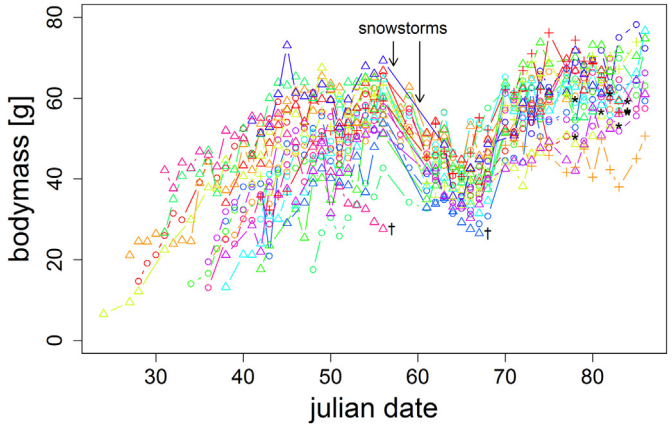

Fig. 8. Body mass development of Wilson's storm petrel nestlings during the breeding season 2017. The 24 observed chicks increased their body masses with age during the breeding season 2017. Two snowstorm incidents caused massive weight loss in all chicks. All but one regained their mass until fledging.*Indicate fledged chicks, †indicate chicks that died during the study. Arrows show snowstorm incidents. Each chick is presented by one colour – symbol combination.

the majority of measurements lay between 38 and 42 °C. According to Prinzinger et al. (1991) these values would cluster in the range of birds in the active (41.02 °C ± 1.29 °C) and resting (38.54 °C ± 0.96 °C) phase of the day and well within the range of body temperatures reported for other small petrels (Warham, 1973). The chicks of this study were only measured in the nest, during their development before fledging. On several occasions we found hypotherm chicks with temperatures as low as 17 °C, which is slightly lower than minimal temperatures for birds in hypothermia found in other studies (Krüger et al., 1982; Prinzinger et al., 1991), or than the 22.5 °C calculated by Geiser and Ruf in their review for birds weighing about 40 g (minimal body temperature during torpor for 40 g bird = 30.2 + 5.53 $\log_{10}(0.04)$ = 22.5; Ruf and Geiser, 2015; Ruf, pers. comm.). But it is higher than the minimum of 10.6 °C reported for fork-tailed storm-petrels (Boersma, 1986). We found hypotherm chicks mainly until they were 45 days old, and hardly during their last two weeks of development, and their general body temperature raised with age (Fig. 2; Table 3). During their development many Wilson's storm-petrel nestlings reached weights exceeding that of their parents by far, without being fully grown (Fig. 8). This, and a following mass loss before fledging is a common pattern in Procellariiformes nestlings (Hamer et al., 2001; Mauck and Ricklefs, 2005; Obst and Nagy, 1993; Phillips and Hamer, 1999). Studies on northern fulmars have shown that Procellariiformes chicks accumulated fat until reaching peak mass, but retain this fat even during mass loss prior to fledging (Phillips and Hamer, 1999). Mass loss for northern fulmars seems to be caused by less frequent feedings by their parents during those last days at the nest (Phillips and Hamer, 1999). In Wilson's storm-petrels studies on energy budget of nestlings suggested a need for energy from lipid reserves (Obst and Nagy, 1993). However, different energetic demands may not be surprising compared to this 20-fold bigger bird. Additionally we found no indication that chicks were starved before leaving the nests. On the contrary, regular nest attendance and feedings until the last recorded day were frequent (unpublished data). Hence, mass loss during this phase is rather interpreted by high energy demands because wing and feather growth, and pre-fledging exercises that are common in burrow-nesting seabirds (Miskelly et al., 2009). Higher body temperatures would go hand in hand with this increased activity pattern, and improved insulation and surface-area volume ratios, and is also known from other seabirds (Ricklefs and Roby, 1983; Weathers et al., 2000). While especially late- born juvenile garden dormice use hypothermia to fatten up before hibernation (Mahlert et al., 2018), Wilson's storm-petrel chicks seem to need their time at the nest to terminate growth, and prepare fledging. Hypothermia would be unfavorable in this situation.

4.2. Influence of feeding and body condition

Provisioning of Wilson's storm-petrel chicks occurred on average on three out of four days and parents provided their chicks with about 6 g of food per night for the observed period of time (Table 4). This is slightly higher than what was calculated for Wilson's storm-petrel chicks at South Georgia (Croxall et al., 1988), but lower than observed at the same colony between 1996 and 2002 (Büßer et al., 2004). If chicks were fed during the previous night their body temperature was higher (Table 3), and chicks with higher body conditions had higher body temperatures. We found that after a fasting for at least one day, chicks' body temperatures decreased with decreasing body conditions (Fig. 5). Many studies showed the opposite trend: animals with better body conditions used hypothermia more frequently (e.g. Rojas et al., 2014; Stawski and Geiser, 2010). The reason for that discrepancy is based on the analysis of adults during non-reproductive times. Thus, adults did not face the trade-off between conserving energy versus growth and development of themselves or their young. Rather feeding imposed the potential of being predated, and fasting an opportunity to prevent predation. Hence, only animals in good conditions are able to abstain from foraging and this way decrease the risk of predation, while animals in bad conditions will need to search and find food in order to survive. However, Chicks on the other hand cannot influence whether they will receive food or not, and for them the most important is to survive the hatchling time until fledging. Only when survival is threatened by starvation it would be advantageous to lower their metabolic rate and to conserve their remaining energy resources. Studies on other storm-petrels came to similar conclusions, hypothermia was reported to occur after fasting or weather events that had presumably negative impact on provisioning (Boersma, 1986; Watson, 2013). This is additionally supported by the fact that after only one or two days of fasting a majority of chicks were still normotherm, while after three or more days hypothermia became more frequent and only few chicks maintained active body temperatures (Figs. 6, 7, Table 1). If structural development is completed and the main aim is to gain fat reserves, hypothermia was shown to successfully bridge times of scarce food, and allow intermittently fastened juvenile garden dormice to gain weight at similar rates than those fed ad libitum (Giroud et al., 2014). For Wilson's storm-petrel chicks structural growth does not finish until fledging (unpublished data). Together with the strong seasonality of the Antarctic it might be dangerous for chicks to be hypothermic too frequently: food abundance seems to be an important factor for growth rates in Wilson's storm-petrel chicks, and is decreasing towards autumn. After rapid growth of late-hatched chicks development becomes slower towards the end of the season when resources are probably declining (Quillfeldt and Peter, 2000). A delay in growth might result in a lower degree of development at fledging or adults leaving the breeding colony before chicks are fledged. Compared to data from 1996 to 2003 breeding seasons in especially 2015 and 2016 were late (Büßer et al., 2004). While nests are blocked with ice and snow petrels cannot start breeding. Studies on garden dormice showed that even though late-born juveniles showed enhanced growth rates, they could not completely catch up with their earlier born conspecifics (Stumpfel et al., 2017). This restriction is most likely also true for Antarctic storm-petrels. Hence, with an already delayed start uninterrupted development becomes even more important. For the future climatologists predict higher snow fall for western Antarctica and the peninsula, caused by warmer air temperatures and higher water evaporation (Turner et al., 2014). Snow fall in spring and shortly before the breeding season starts could delay egg-laying and cause an unfavorable initial situation for chick survival.

Literature of naturally occurring irregular feeding and its influence

on hyothermia is scarce. However, Superina and Jahn (2013) found that armadillos feeding on low quality food, spent prolonged times hypothermic compared to those individuals fed with high quality food. This nutritional challenge might be comparable to that of chicks facing irregular feeding intervals, as both will lead to a worse body condition. We could not control for different food qualities among chicks in this study, but former studies investigating diet compositions of Wilson's storm-petrel chicks and adults reported a general pattern of preferred food items at different times during the breeding cycle instead of individual differences (Quillfeldt, 2002b). Hypothermia thus postpones and by that possibly reduces the risk of starvation. After the extended resting time at very low energy expenditures armadillos might find food of higher quality, while petrel chicks might be fed by their returning parents again. Like in fork-tailed storm-petrels facultative hypothermia in Wilson's storm-petrels could be an adaption to the frequently found gorge-and-fast provisioning pattern, as a combination of hypothermia during fasting to avoid maintenance costs for endothermy, and rapid growth after large meals could make up for development delay during hypothermia (Boersma, 1986).

4.3. Influence of environmental conditions

During severe environmental conditions, like low ambient temperature or high wind speed, other authors reported enhanced hypothermic behavior (Dietz and Kalko, 2006; Geiser, 2004, 1988; Watson, 2013). In our study we could not find such an influence of maximal nocturnal wind speed on Wilson's storm-petrel chicks' body temperature, but minimal nocturnal temperatures influenced their body temperatures negatively. As they grow up in the extreme environment of Antarctica Wilson's storm-petrel chicks experience low temperatures on a daily basis. Temperature extremes during the night differed over the years by only about 3 °C above and below the mean minimal temperature. This difference is potentially even smaller inside the cavities where the chicks are raised. For other burrow-nesting petrels breeding in sub-Antarctic regions outside temperatures did not or only slightly influence metabolic rates of birds (Adams and Brown, 1984). This could be true for Wilson's storm-petrel nestlings as well. Possibly chicks start moving more when temperatures drop slightly to find a better spot within the nest, and produce this way more heat in general. While it influences body temperature in general, it is less likely to be one of the main drivers for hypothermia for this species.

Long fasting periods occurred at all times, but especially after snowstorms. With an predicted increase of snow-fall in western Antarctic areas and the peninsula, snow storms are assumed to occur more frequently due to climate change (Turner et al., 2014). For the present data of 2017 nests were often accessible again after one to three days. Most chicks were fed already soon after such an event, but many chicks experienced a time of irregular feedings for the following days with long fasting times that in one case led to starvation of a chick in 2017. Especially young chicks often die during this entombment and the following fasting (Büßer et al., 2004; own observation). Surviving chicks became often hypothermic within few days after the storm, while they were often observed to be normothermic directly after the storm. Hypothermic responses can therefore not be linked directly to food shortages due to blockage of nests. However, as this pattern was shown for the majority of the breeding colony it still seems to be a valuable explanation that the poor provisioning's main factor was the snowstorm. As it is common for long lived animals, it is also known for storm-petrels to first care for themselves when in bad conditions, before provisioning their chicks again (Quillfeldt and Möstl, 2003). After snowstorms adults hence might be in a poor nutritional state themselves and may need to ensure their own survival before being able to regularly provide for their offspring again. This pattern was also found for another petrel species, the Antarctic petrel (*Thalassoica Antarctica*, Tveraa et al., 1998). It was shown that Antarctic petrel adults in good conditions fed larger meals to their chicks. Their chicks had better conditions themselves, and were more likely to survive than those of birds starting the experiment in worse body conditions. Within the next ten days after the snowstorm all chicks except one were fed regularly again, could increase body mass, and fledge. However, several snowstorms during one season could undermine chicks' fat reserves, and frequent hypothermic responses could delay development and put chicks at risk for successful fledging.

5. Conclusions

Body and torpor temperatures of Wilson's storm-petrel chicks fit well into the range of other animals of comparative size and activity. Hypothermic responses mirrors very closely the challenges Wilson's storm-petrel chicks face during their development: if provisioning is regular chicks maintain high body temperatures. However, the more unpredictable provisioning is, the more frequent hypothermia is observed in the chicks. The possibility of this strategy enables the chicks to survive dangerous times of limited food supply for example due to snowstorms. Thus this behavior may be especially important in years to come as climate change is predicted to increase snow fall in their breeding area, the Antarctic peninsula, and hence increase chances of blocked nests during the breeding season (Turner et al., 2014). As torpor usage enabled most chicks to survive extended times of unpredicted provisioning a next step will be to investigate if using torpor more frequently will have negative impacts for their future lives, for example because a decreased time for development forces them to fledge in a poorer body condition (compare Quillfeldt and Peter, 2000).

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References

Adams, N.J., Brown, C.R., 1984. Metabolic rates of sub-antarctic procellariiformes: a comparative study. Comp. Biochem. Physiol. 77, 169–173. https://doi.org/10.1016/0300-9629(84)90030-6.

Audet, D., Fenton, M.B., 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera Vespertilionidae): a field study. Physiol. Zool. 61, 197–204. https://doi.org/10.1086/physzool.61.3.30161232.

Bae, H.H., Larkin, J.E., Zucker, I., 2003. Juvenile Siberian hamsters display torpor and modified locomotor activity and body temperature rhythms in response to reduced food availability. Physiol. Biochem. Zool. 76, 858–867. https://doi.org/10.1086/381462.

Bates, D., Mächler, M., Bolker, B.M., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beck, J.R., Brown, M.A., Brown, D.W., 1972. The biology of Wilson's storm petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. In: British Antarctic Survey: Scientific Reports.

Blumberg, M.S., Sokoloff, G., 1998. Thermoregulatory competence and behavioral expression in the young of altricial species - Revisited. Dev. Psychobiol. 33, 107–123. https://doi.org/10.1002/(SICI)1098-2302(199809)33:2<107::AID-DEV2>3.0.CO;2-N.

Boersma, P.D., 1986. Body temperature, torpor, and growth in chicks of fork-tailed storm-petrels (*Oceanodroma furcata*). Physiol. Zool. 59, 10–19. https://doi.org/10.1017/CBO9781107415324.004.

Boersma, P.D., Wheelwright, N.T., 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed storm-petrel. Condor 81, 157–165. https://doi.org/10.2307/1367282.

Büßer, C., Kahles, A., Quillfeldt, P., 2004. Breeding success and chick provisioning in Wilson's storm-petrels *Oceanites oceanicus* over seven years: frequent failures due to food shortage and entombment. Polar Biol. 27, 613–622. https://doi.org/10.1007/s00300-004-0627-z.
Cossins, A.R., Prosser, C.L., 1978. Evolutionary adaptation of membranes to temperature. Proc. Natl. Acad. Sci. 75, 2040–2043. https://doi.org/10.1073/pnas.75.4.2040.
Croxall, J.P., Hill, H.J., Lidstone-Scott, R., O'Connell, M.J., Prince, P.A., 1988. Food and feeding ecology of Wilson's storm petrel *Oceanites oceanicus* at South Georgia. J. Zool. 216, 83–102. https://doi.org/10.1111/j.1469-7998.1988.tb02417.x.
Dietz, M., Kalko, E.K.V., 2006. Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). J. Comp. Physiol. B 176, 223–231. https://doi.org/10.1007/s00360-005-0043-x.
Doucette, L.I., Brigham, R.M., Pavey, C.R., Geiser, F., 2012. Prey availability affects daily torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Oecologia 169, 361–372. https://doi.org/10.1007/s00442-011-2214-7.
Eichhorn, G., Groscolas, R., Le Glaunec, G., Parisel, C., Arnold, L., Medina, P., Handrich, Y., 2011. Heterothermy in growing king penguins. Nat. Commun. 2, 435. https://doi.org/10.1038/ncomms1436.
Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, Second ed. Sage, Thousand Oaks, CA.
Gębczyński, A.K., 1995. Is there a hypothermia in Wilson's storm petrel chicks? Polish Polar Res. 16, 175–184.
Geiser, F., 1988. Daily torpor and thermoregulation in *Antechinus* (Marsupialia): influence of body mass, season, development, reproduction, and sex. Oecologia 77, 395–399. https://doi.org/10.1007/BF00378050.
Geiser, F., 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clin. Exp. Pharmacol. Physiol. 25, 736–740. https://doi.org/10.1111/j.1440-1681.1998.tb02287.x.
Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu. Rev. Physiol. 66, 239–274. https://doi.org/10.1146/annurev.physiol.66.032102.115105.
Geiser, F., Brigham, R.M., 2012. The other functions of torpor. In: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 109–121. https://doi.org/10.1007/978-3-642-28678-0.
Giroud, S., Zahn, S., Criscuolo, F., Chery, I., Blanc, S., Turbill, C., Ruf, T., 2014. Late-born intermittently fasted juvenile garden dormice use torpor to grow and fatten prior to hibernation: consequences for ageing processes. Proc. R. Soc. B Biol. Sci. 281, 20141131. https://doi.org/10.1098/rspb.2014.1131.
Gladbach, A., Braun, C., Nordt, A., Peter, H.-U., Quillfeldt, P., 2009. Estimation of feeding frequencies by periodic weighing of chicks: evaluation by video-observation of burrow- nesting Wilson's Storm-Petrels (*Oceanites oceanicus*). EMU 109, 316–320. https://doi.org/10.1071/MU09043.
Hainsworth, F.R., Collins, B.G., Wolf, L.L., 1977. The function of torpor in hummingbirds. Physiol. Zool. 50, 215–222. https://doi.org/10.1086/physzool.50.3.30155724.
Hamer, K.C., Schreiber, E.A., Burger, J., 2001. Breeding biology, life histories, and life history–environment interactions in seabirds. In: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, FL, pp. 217–261.
Heldmaier, G., Neuweiler, G., Rössler, W., 2013,Springer;. Vergleichende Tierphysiologie. Heidelberg,, Berlin.
Hochachka, P.W., Somero, G.N., 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, New York.
Hwang,, Y. Ten, Larivière, S., Messier, F., 2007. Energetic consequences and ecological significance of heterothermy and social thermoregulation in striped skunks (*Mephitis mephitis*). Physiol. Biochem. Zool. 80, 138–145. https://doi.org/10.1086/509211.
Jensen, C., Bech, C., 1992. Oxygen consumption and acid-base balance during shallow hypothermia in the pigeon. Respir. Physiol. 88, 193–204. https://doi.org/10.1016/0034-5687(92)90040-4.
Krüger, K., Prinzinger, R., Schuchmann, K.-L., 1982. Torpor and metabolism in hummingbirds. Comp. Biochem. Physiol. A 73, 679–689. https://doi.org/10.1016/0300-9629(82)90275-4.
Kunz, T.H., 1988. Methods of assessing the availability of prey to insectivorous bats. In: Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, D. C.; London, pp. 191–210. https://doi.org/10.2307/1381698.
Mahlert, B., Gerritsmann, H., Stalder, G., Ruf, T., Zahariev, A., Blanc, S., Giroud, S., 2018. Implications of being born late in the active season for growth, fattening, torpor use, winter survival and fecundity. elife 7, 1–25. https://doi.org/10.7554/eLife.31225.
Mauck, R.A., Ricklefs, R.E., 2005. Control of fledging age in Leach's Storm-Petrel, *Oceanodroma leucorhoa*: chick development and prefledging mass loss. Funct. Ecol. 19, 73–80. https://doi.org/10.1111/j.0269-8463.2005.00933.x.
McAllan, B.M., Geiser, F., 2014. Torpor during reproduction in mammals and birds: Dealing with an energetic conundrum. Integr. Comp. Biol. 54, 516–532. https://doi.org/10.1093/icb/icu093.
McKechnie, A.E., Lovegrove, B.G., 2002. Avian facultative hypothermic responses: A review. Condor 104, 705–724.
Miskelly, C.M., Taylor, G.A., Gummer, H., Williams, R., 2009. Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*: Family Procellariidae). Biol. Conserv. 142, 1965–1980. https://doi.org/10.1016/j.biocon.2009.03.027.
Nichelmann, M., Tzschentke, B., 2002. Ontogeny of thermoregulation in precocial birds. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 131, 751–763.
Nichelmann, M., Burmeister, A., Janke, O., Höchel, J., Tzschentke, B., 1998. Avian embryonic thermoregulation: role of Q10 in interpretation of endothermic reactions. J. Therm. Biol. 23, 369–376.
Obst, B.S., Nagy, K.A., 1993. Stomach oil and the energy budget of Wilson's storm-petrel nestlings. Condor 95, 792–805. https://doi.org/10.2307/1369418.
Phillips, R.A., Hamer, K.C., 1999. Lipid reserves, fasting capability and the evolution of nestling obesity in procellariiform seabirds. Proc. R. Soc. B Biol. Sci. 266, 1329. https://doi.org/10.1098/rspb.1999.0783.
Prinzinger, R., Preßmar, A., Schleucher, E., 1991. Mini review - body temperature in birds. Comp. Biochem. Physiol. Part A Physiol. 99, 499–506. https://doi.org/10.1016/0300-9629(91)90122-S.
Quillfeldt, P., 2001. Variation in breeding success in Wilson's storm petrels: influence of environmental factors. Antarct. Sci. 13, 400–409. https://doi.org/10.1017/S0954102001000566.
Quillfeldt, P., 2002a. Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. Anim. Behav. 64, 579–587. https://doi.org/10.1006/anbe.2002.3090.
Quillfeldt, P., 2002b. Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands. Polar Biol. 25, 216–221. https://doi.org/10.1007/s00300-001-0332-0.
Quillfeldt, P., 2006. Wilson's Storm-Petrel. Encycl, Antarct.
Quillfeldt, P., Möstl, E., 2003. Resource allocation in Wilson's storm-petrels *Oceanites oceanicus* determined by measurement of glucocorticoid excretion. Acta Ethol. 5, 115–122. https://doi.org/10.1007/s10211-003-0074-9.
Quillfeldt, P., Peter, H.-U., 2000. Provisioning and growth in chicks of Wilson's storm-petrels (*Oceanites oceanicus*) on King George Island, South Shetland Islands. Polar Biol. 23, 817–824. https://doi.org/10.1007/s003000000158.
Whittow, P.A., 1981. Environmental factors affecting the length of gestation in mammals. In: Gilmore, D., Cook, B. (Eds.), *Environmental Factors in Mammal Reproduction*. Palgrave Macmillan, UK, London, pp. 199–213. https://doi.org/10.1007/978-1-349-03964-7_14.
Racey, P.A., Swift, S.M., 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. J. Repord. Fertil. 61, 123–129.
Ransome, R.D., 1989. Population changes of Greater horseshoe bats studied near Bristol over the past twenty-six years. Biol. J. Linn. Soc. 38, 71–82. https://doi.org/10.1111/j.1095-8312.1989.tb01564.x.
Ricklefs, R.E., Roby, D.D., 1983. Development of homeothermy in the diving petrels *Pelecanoides urinatrix exsul* and *P. georgicus*, and the Antarctic prion *Pachyptila desolata*. Comp. Biochem. Physiol. A Physiol. 75, 307–311.
Roberts, B., 1941. The Life Cycle of Wilson's Petrel *Oceanites oceanicus* (Kuhl). British Graham Land Expedition, pp. 1934–1937.
Rojas, A.D., Körtner, G., Geiser, F., 2014. Torpor in free-ranging antechinus: Does it increase fitness? Naturwissenschaften 101, 105–114. https://doi.org/10.1007/s00114-013-1136-0.
Ruf, T., Geiser, F., 2015. Daily torpor and hibernation in birds and mammals. Biol. Rev. 90, 891–926. https://doi.org/10.1111/brv.12137.
Ruf, T., Stieglitz, A., Steinlechner, S., Blank, J.L., Heldmaier, G., 1993. Cold exposure and food restriction facilitate physiological responses to short photoperiod in Djungarian hamsters (*Phodopus sungorus*). J. Exp. Zool. 267, 104–112. https://doi.org/10.1002/jez.1402670203.
Schleucher, E., Withers, P.C., 2002. Metabolic and thermal physiology of pigeons and doves. Physiol. Biochem. Zool. 75, 439–450. https://doi.org/10.1086/342803.
Somero, G.N., 1995. Proteins and Temperature. Annu. Rev. Physiol. 57, 43–68. https://doi.org/10.1146/annurev.ph.57.030195.000355.
Stawski, C., Geiser, F., 2010. Fat and fed: Frequent use of summer torpor in a subtropical bat. Naturwissenschaften 97, 29–35. https://doi.org/10.1007/s00114-009-0606-x.
Stumpfel, S., Bieber, C., Blanc, S., Ruf, T., Giroud, S., 2017. Differences in growth rates and pre-hibernation body mass gain between early and late-born juvenile garden dormice. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 187, 253–263. https://doi.org/10.1007/s00360-016-1017-x.
Superina, M., Jahn, G.A., 2013. Effect of low-quality diet on torpor frequency and depth in the pichi *Zaedyus pichiy* (Xenarthra, Dasypodidae), a South American armadillo. J. Therm. Biol. 38, 280–285. https://doi.org/10.1016/j.jtherbio.2013.03.004.
The R Core Team, 2018. : A Language and Environment for Statistical Computing.
Turner, J., Barrand, N.E., Bracegirdle, T.J., Convey, P., Hodgson, D.A., Jarvis, M., Jenkins, A., Marshall, G., Meredith, M.P., Roscoe, H., Shanklin, J., French, J., Goosse, H., Guglielmin, M., Gutt, J., Jacobs, S., Kennicutt, M.C., Masson-Delmotte, V., Mayewski, P., Navarro, F., Robinson, S., Scambos, T., Sparrow, M., Summerhayes, C., Speer, K., Klepikov, A., 2014. Antarctic climate change and the environment: An update. Polar Rec. 50, 237–259. https://doi.org/10.1017/S0032247413000296.
Tveraa, T., Sæther, B.E., Aanes, R., Erikstad, K.E., 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. J. Anim. Ecol. 67, 699–704. https://doi.org/10.1046/j.1365-2656.1998.00234.x.
Vleck, C.M., Kenagy, G.J., 1980. Embryonic metabolism of the fork-tailed storm petrel: physiological patterns during prolonged and interrupted incubation. Physiol. Zool. 53, 32–42, https://doi.org/10.1086/physzool.53.1.30155773.
Warham, J., 1973. Body temperatures of petrels. Condor 73, 214–219.
Watson, H., 2013. The occurrence of hypothermia in nestlings of the European Storm-petrel *Hydrobates pelagicus*. Seabird 26, 96–99.
Weathers, W.W., Gerhart, K.L., Hodum, P.J., 2000. Thermoregulation in Antarctic fulmarine petrels. J. Comp. Physiol. B. 170, 561–572. https://doi.org/10.1007/s003600000134.
Wheelwright, N.T., Boersma, P.D., 1979. Egg chilling and the thermal environment of the Fork-tailed storm petrel (*Oceanodroma furcata*) nest. Physiol. Zool. 52, 231–239. https://doi.org/10.1086/physzool.52.2.30152566.
Whittow, G.C., 2001. Seabird reproductive physiology and energetics. In: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, FL, pp. 409–437.
Wojciechowski, M.S., Jefimow, M., Tegowska, E., 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 147, 828–840. https://doi.org/10.1016/j.cbpa.2006.06.039.